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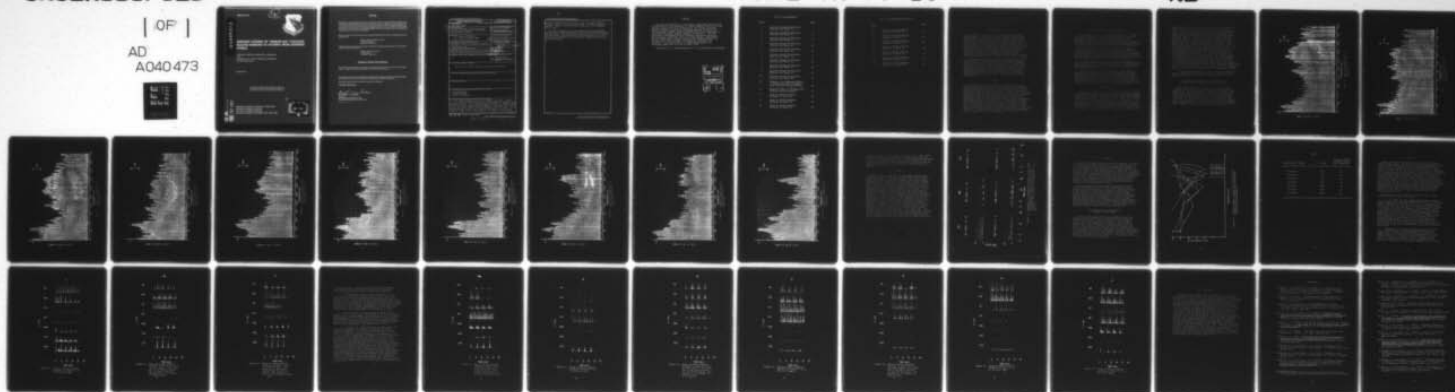
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RESPONSE PATTERNS OF "PRIMARY-LIKE" COCHLEAR NUCLEUS NEURONS TO EXCERPTS FROM SUSTAINED VOWELS

AEROSPACE MEDICAL RESEARCH LABORATORY
AND
UNIVERSITY OF DAYTON RESEARCH INSTITUTE
DAYTON, OHIO 45469

MARCH 1977

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TECHNICAL REVIEW AND APPROVAL

The experiments reported herein were conducted according to the "Guide for the Care and Use of Laboratory Animals," Institute of Laboratory Animal Resources, National Research Council.

This report has been reviewed by the Information Office (OI) and is releasable to the National Technical Information Service (NTIS). At NTIS, it will be available to the general public, including foreign nations.

This technical report has been reviewed and is approved for publication.

FOR THE COMMANDER



HENNING E. VON GIERKE
Director
Biodynamics and Bionics Division
Aerospace Medical Research Laboratory

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19 REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM	
1. REPORT NUMBER	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER	
18 AMRL TR-77-10			
4. TITLE (and Subtitle)		5. TYPE OF REPORT & PERIOD COVERED	
6 RESPONSE PATTERNS OF "PRIMARY-LIKE" COCHLEAR NUCLEUS NEURONS TO EXCERPTS FROM SUSTAINED VOWELS		9 Technical rept. Jan 72 — Jan 77	
7. AUTHOR(s)		6. PERFORMING ORG. REPORT NUMBER	
10 Thomas J. Moore* John L. Cashin, Jr.**			
9. PERFORMING ORGANIZATION NAME AND ADDRESS		8. CONTRACT OR GRANT NUMBER(s)	
*Aerospace Medical Research Laboratory & **University of Dayton Research Institute, Dayton OH 45469		15 F33615-76-C-0510 new	
10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS		17 62202F, 7233-03-02 16 7233-03-33	
11. CONTROLLING OFFICE NAME AND ADDRESS		12. REPORT DATE	
Aerospace Medical Rsch Laboratory, Aero- space Medical Division, Air Force Systems Command, Wright-Patterson AFB OH 45433		11 March 1977	
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		13. NUMBER OF PAGES	
		12 41 p.	
		14. SECURITY CLASS. (of this report)	
		UNCLASSIFIED	
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE	
16. DISTRIBUTION STATEMENT (of this Report)			
Approved for public release; distribution unlimited.			
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)			
18. SUPPLEMENTARY NOTES			
19. KEY WORDS (Continue on reverse side if necessary and identify by block number)			
Neurophysiology Auditory System Speech Processing			
20. ABSTRACT (Continue on reverse side if necessary and identify by block number)			
<p>This report compares the neural response patterns of eighth nerve and "primary-like" cochlear nucleus neurons to excerpts from sustained vowels. The dominant intervals defined by neural firings within each pitch period of the response to the vowels were found to be the same in eighth nerve and "primary-like" CN units. These intervals were found to be related to the pitch rate and first formant values of the vowels employed as stimuli. This finding</p> <p>(cont on p 14733)</p>			

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→ provides support for the contention that the auditory system performs a temporal analysis rather than a frequency analysis of signals. (Moore, 1974; Mundie and Goldstein, 1971; Nordmark, 1968, 1970).

→ The data gathered in these neurophysiological experiments are employed in developing design criteria for speech recognition systems based on the performance characteristics of the auditory nervous system. Such systems would be a valuable tool to the Air Force in the fields of intelligence, communications and man-machine interface.

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PREFACE

The research reported in this paper covers work done jointly by personnel of the University of Dayton Research Institute under Contract F33615-76-C-0510 sponsored by the 6570th Aerospace Medical Research Laboratory, Aerospace Medical Division, Air Force Systems Command, Wright-Patterson AFB OH and personnel of the 6570th Aerospace Medical Research Laboratory. The work performed by Aerospace Medical Research Laboratory personnel was initiated under Work Unit 02 of Task 723303, "Development of New Techniques of Signal Detection and Preprocessing," of Project 7233, "Applications of Biological Principles as Solutions to Air Force Needs in Signal Processing," and continued under Work Unit 33 of Task 723303.

The advice of J. Ryland Mundie, M.D. is gratefully acknowledged.

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INTRODUCTION

For a number of years this laboratory has been employing human speech as a test signal for the auditory system. Speech has been employed because it provides a complex stimulus which varies in time along the dimensions of frequency and amplitude. The response of various parts of the auditory system to this complex input is much more rich and diversified than the response to more classical input signals, e.g., pure tones and clicks. Other investigators (Casparry, et al, 1974; Kiang and Moxon, 1974; Rupert, et al, 1974, 1976; Watanabi and Sakai, 1973) have also occasionally employed speech signals in their investigations of the auditory system. It is hoped that by employing these stimuli an understanding of stimulus coding and decoding mechanisms in general, as well as ways in which specific acoustic cues in speech are encoded by the auditory system will be gained.

The investigations performed in this laboratory have studied the transforms occurring at the level of the basilar membrane, using an analog cochlea (Godfrey, 1972 a, b, 1974; Mundie and Moore, 1967, 1968 a, b, 1970), at the level of the eighth nerve (Goldstein and Mundie, 1971, 1972; Mundie, et al, 1974) and at the level of the cochlear nucleus (Moore and Cashin, 1974, 1976). The present report will attempt to demonstrate that temporal information considered to be an important cue for identifying various speech sounds at the level of the basilar membrane is preserved and enhanced by at least a subpopulation of cochlear nucleus neurons.

METHOD

The experimental animal employed was the albino guinea pig within a weight range of 250-600 grams. Animals were anesthetized with intraperitoneal injections of sodium pentobarbital and maintained with subsequent hourly injections. Neural responses were monitored by means of glass microelectrodes, tip diameter 1-2 microns, that had been vacuum filled with a 3M NaCl solution. The electrodes were inserted into the right cochlear nucleus through an intact cerebellum. This was initially accomplished by computing the necessary stereotactic coordinates from X-rays taken of each experimental animal (Gehrich and Cashin, 1972). Records were maintained and visual examination following successful experiments verified the location of the cochlear nucleus and its position in relation to the internal auditory meatus as located on the X-rays. After numerous experiments standard stereotactic coordinates were developed, which used in conjunction with surface landmarks on the cerebellum enabled us to dispense with the X-rays. Post-experimental verification of electrode position was retained.

A. Data Acquisition and Signal Generation

The recording electrode was manually advanced at a 45° angle from the left surface of the cerebellum to within 0.5 mm of the calculated coordinates of the right cochlear nucleus. The experimenter then left the sound isolated room in which the animal was located and continued to advance the electrode by means of a remote hydraulic microdrive system from an adjacent room which contained the signal generation and data acquisition equipment.

White noise bursts (0 rise-fall times, 100 msec duration, 80 dB SPL, presented twice per second) were used to locate and isolate single unit responses. When a responsive unit was found, its characteristic frequency (CF) and response area were determined by means of pure tone bursts (110 msec duration, 10 msec rise-fall times, presented twice per second). Stimulus frequency was monitored with an electronic counter (Hewlett-Packard Model 5245L).

All stimuli were presented to the animal through a Western Electric 640AA condenser microphone coupled to the external auditory meatus through a hollow earbar in the headholder. This device was acoustically calibrated in situ in terms of sound pressure level (re 0.0002 dyne/cm bar).

The neural potentials to be recorded were passed through a differential dc preamplifier (Transidyne MPA-6) and a bandpass amplifier (Transidyne 1125). The amplified signals were monitored with an oscilloscope and by means of a switching network could either be recorded on digital tape and simultaneously analyzed "on-line" with a PDP-1 computer or be recorded on analog magnetic tape and transferred at a later time. The neural response and its digital representation were displayed on a memoscope (Hughes 105A).

B. Speech Stimuli

While white noise and pure-tone bursts were employed to locate and classify the individual neurons, excerpts from human sustained vowels were the primary stimuli used. These stimuli were generated in the following manner: The speaker (male) produced a CV utterance consisting of one of ten vowels (/i/, /I/, /ε/, /æ/, /a/, /ʌ/, /ɔ/, /o/, /u/, and /r/), always beginning with the consonant /b/. All utterances were monitored with a storage oscilloscope and the peak amplitude in all cases was approximately equal. Using a digital computer (PDP-1) the analog signal from the microphone was digitized at a rate of 25-kilo samples per second, stored in computer memory and reproduced on a computer controlled readout. A segment of the

reproduced signal, at least 50 msec into the sustained vowel, was edited out by means of a light pen attachment to the computer display. This edited segment consisted of a single pitch period of the vowel (approximately 8 msec in duration). The selected samples were then identified and stored in computer memory for later playback in the desired format through a digital-to-analog converter. When the stimuli were recorded on analog tape they were regenerated in strings of five vowel sounds, each vowel sound consisting of five repetitions of the single pitch period excerpted from the original analog signal of that vowel. Each stimulus run had a duration of approximately 200 msec. Since these vowels were excerpted from natural utterances, the duration of each pitch period is not uniform across all vowels. The window during which the neural responses were recorded was a constant 200 msec. Therefore, less than five pitch periods of a neuron's response to the final vowel in each run may have been recorded. Where this occurred it is noted in the caption of the appropriate Figure. The presentation of two sequential runs exposed the neuron to all ten vowel sounds. The analog stimulus tape contained ten such pairs of runs, the order of the vowels in each pair of runs being balanced so that in no two runs was any vowel preceded and followed by the same vowels as in another run. Each run on analog tape was repeated 110 times, each repetition locked to a sync pulse, with a 300 msec wait time between repetitions. After a run had been repeated 110 times, there was a 15 sec pause during which the next run to be presented was identified by number.

Spectral analyses were made of each of the vowel stimuli in order to determine their frequency content. Figures 1-10 depict the spectral energy distribution functions for each of the ten vowels.

COMPARISON OF PRIMARY AND A SUBPOPULATION OF COCHLEAR NUCLEUS NEURONS IN RESPONSE TO SPEECH

Among the many attempts to devise a classification scheme to organize the morphologically (Harrison and Feldman, 1970; Lorenti de No, 1933; Osen, 1969) and functionally (Caspary, 1972; Kiang, et al., 1965; Moushegian and Rupert, 1970 a, b; Pfeiffer, 1966) diverse neuronal population of the cochlear nucleus, one of the more generally accepted is the classification of neurons on the basis of their response pattern to a tone burst at the neuron's CF. On the basis of this scheme neurons in the cochlear nucleus have generally been divided into four classes: "primary-like," "chopper," "pauser," and "on" (Kiang, et al, 1965; Pfeiffer, 1966). Although there are indications in the literature that a

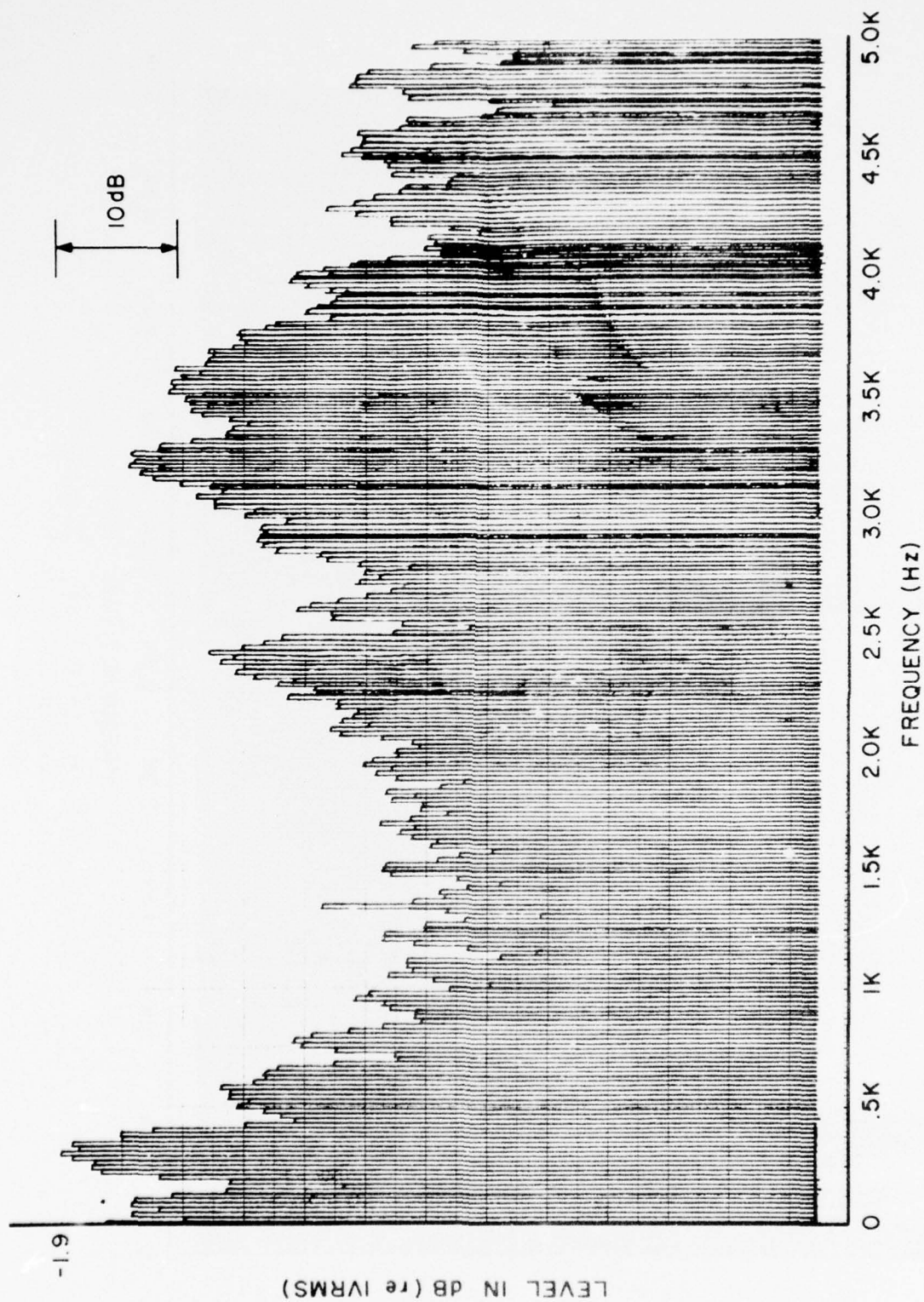


Figure 1. Spectral Energy Distribution Function for Vowel /i/.

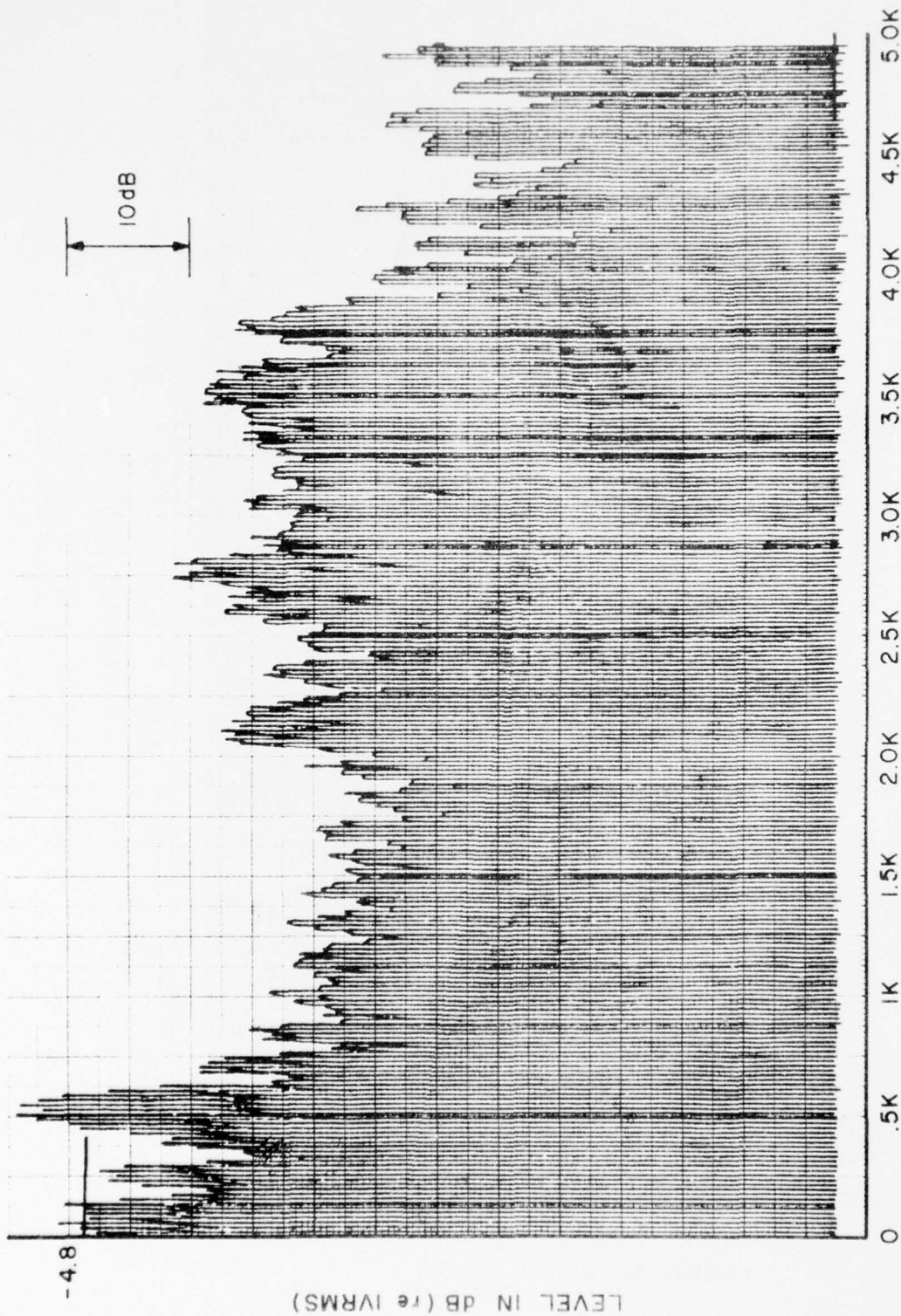


Figure 2. Spectral Energy Distribution Function for Vowel /I/.

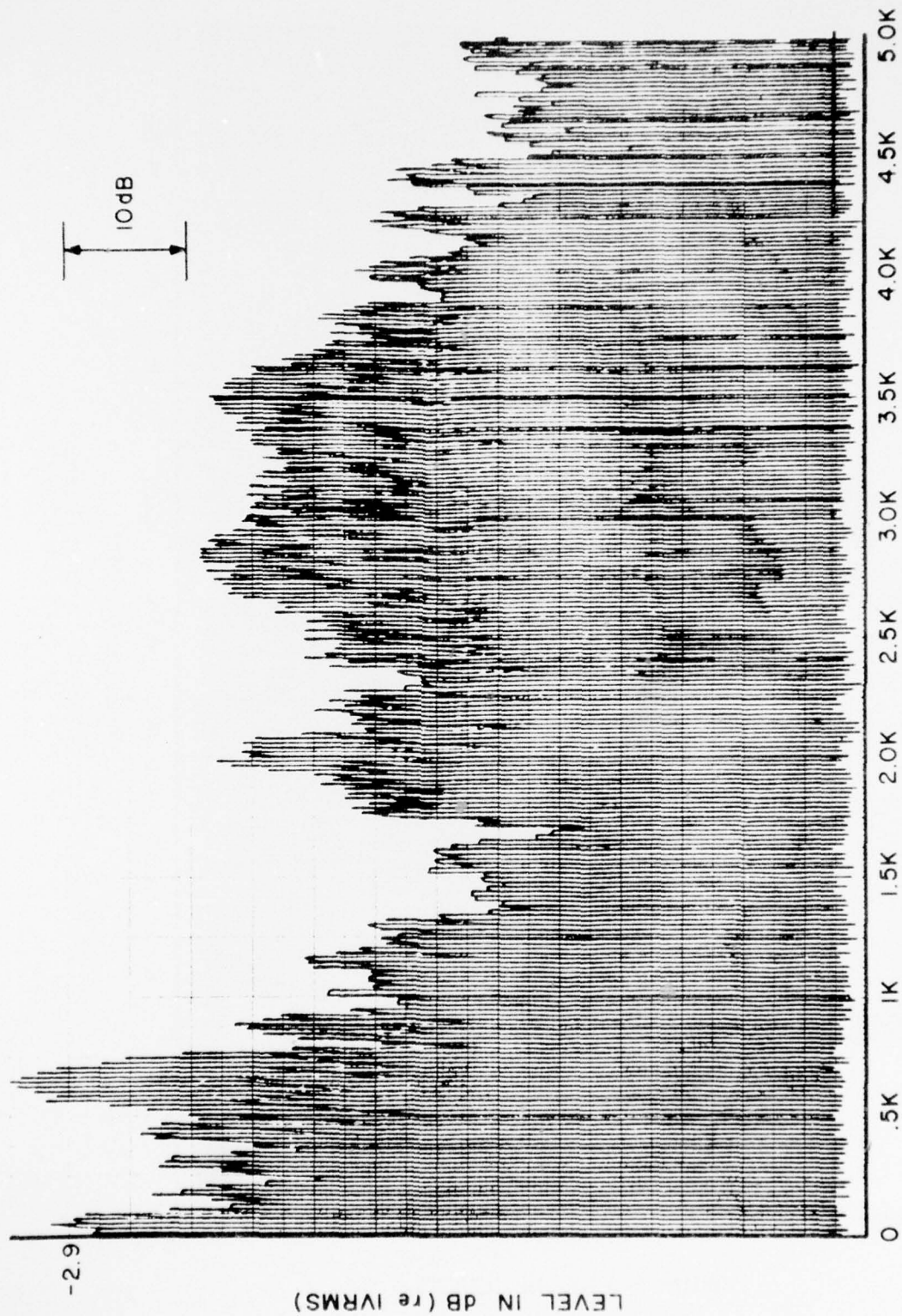


Figure 3. Spectral Energy Distribution Function for Vowel /ε/.

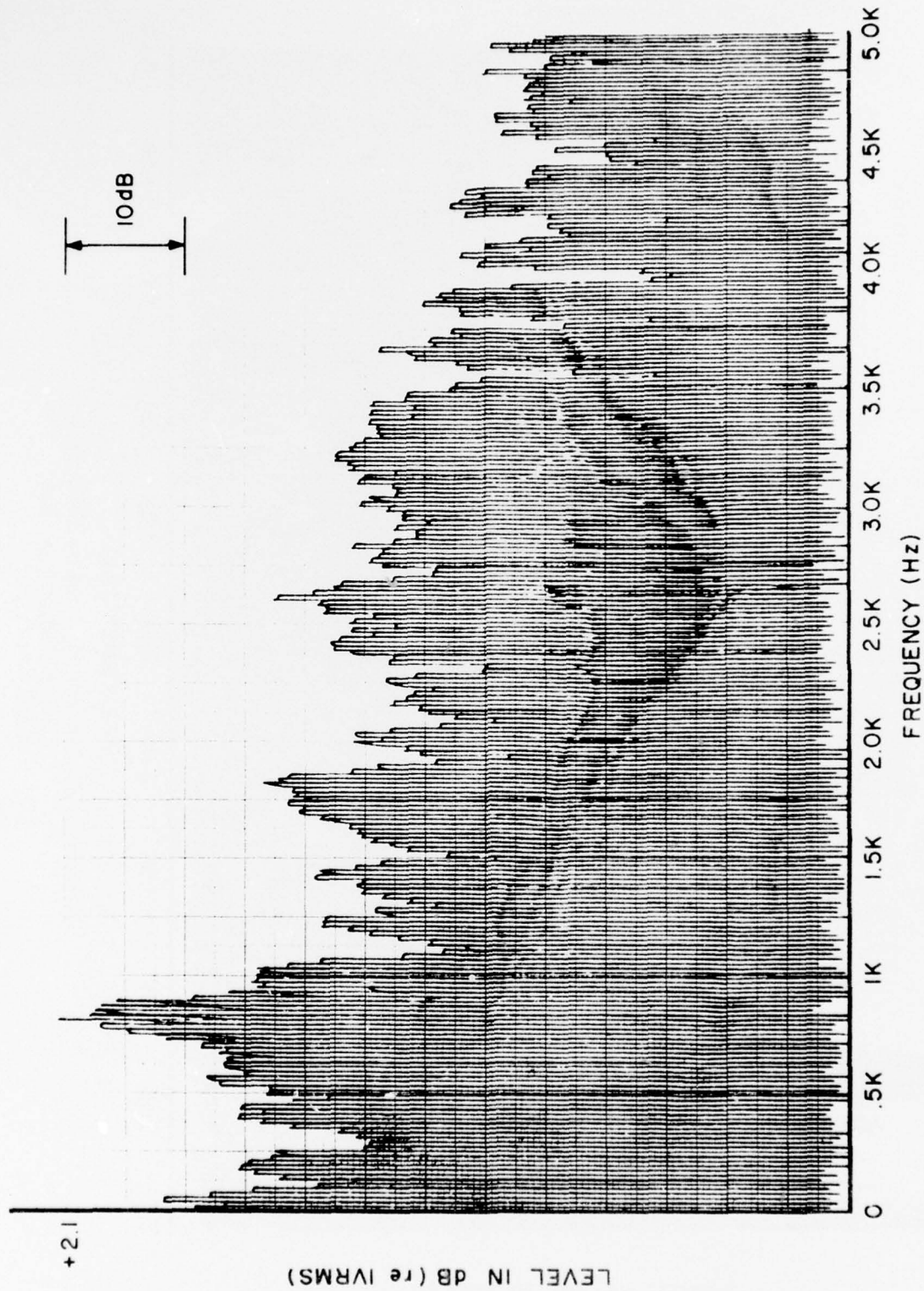


Figure 4. Spectral Energy Distribution Function for Vowel /æ/.

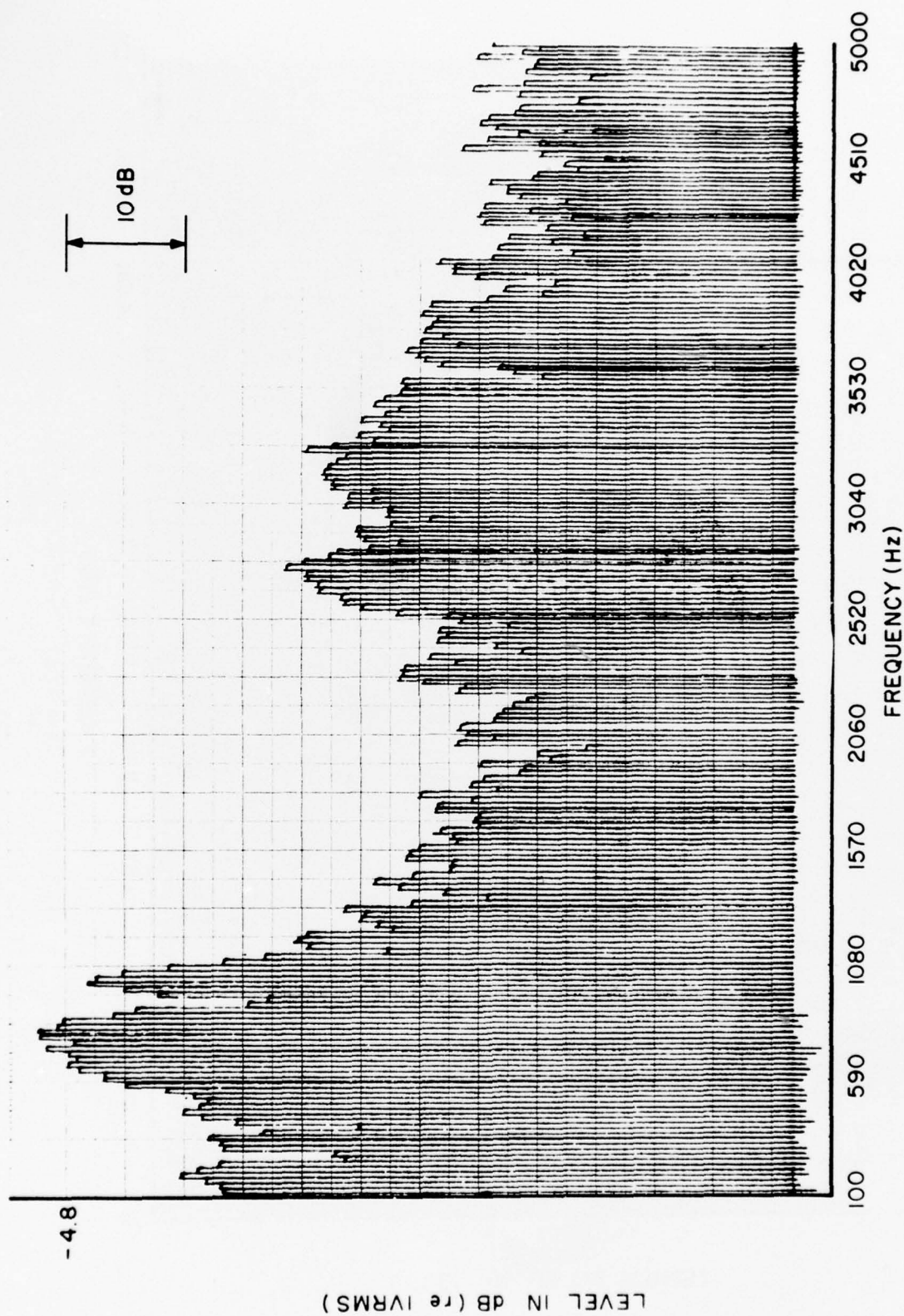


Figure 5. Spectral Energy Distribution Function for Vowel /a/.

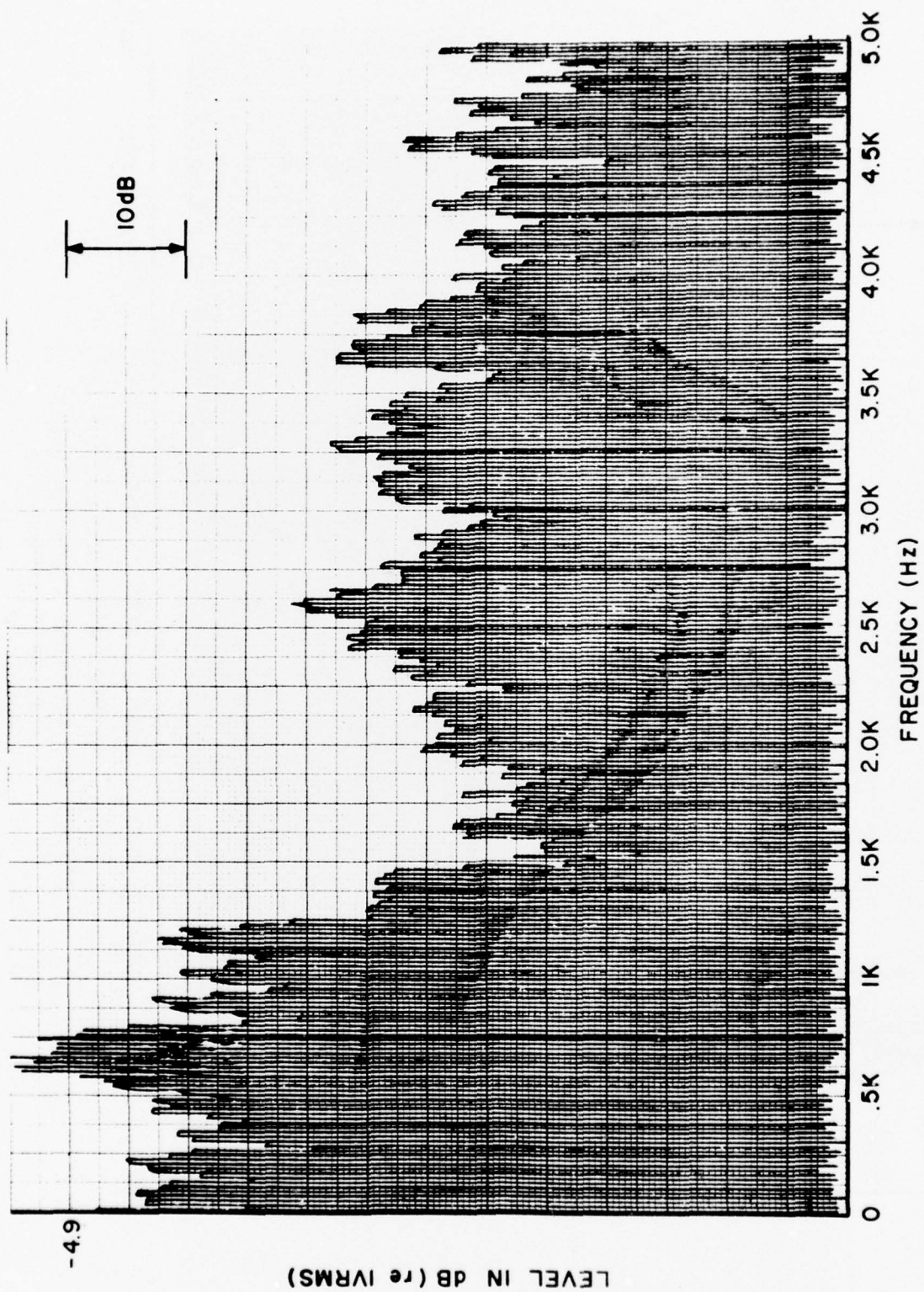


Figure 6. Spectral Energy Distribution Function for Vowel /Λ/.

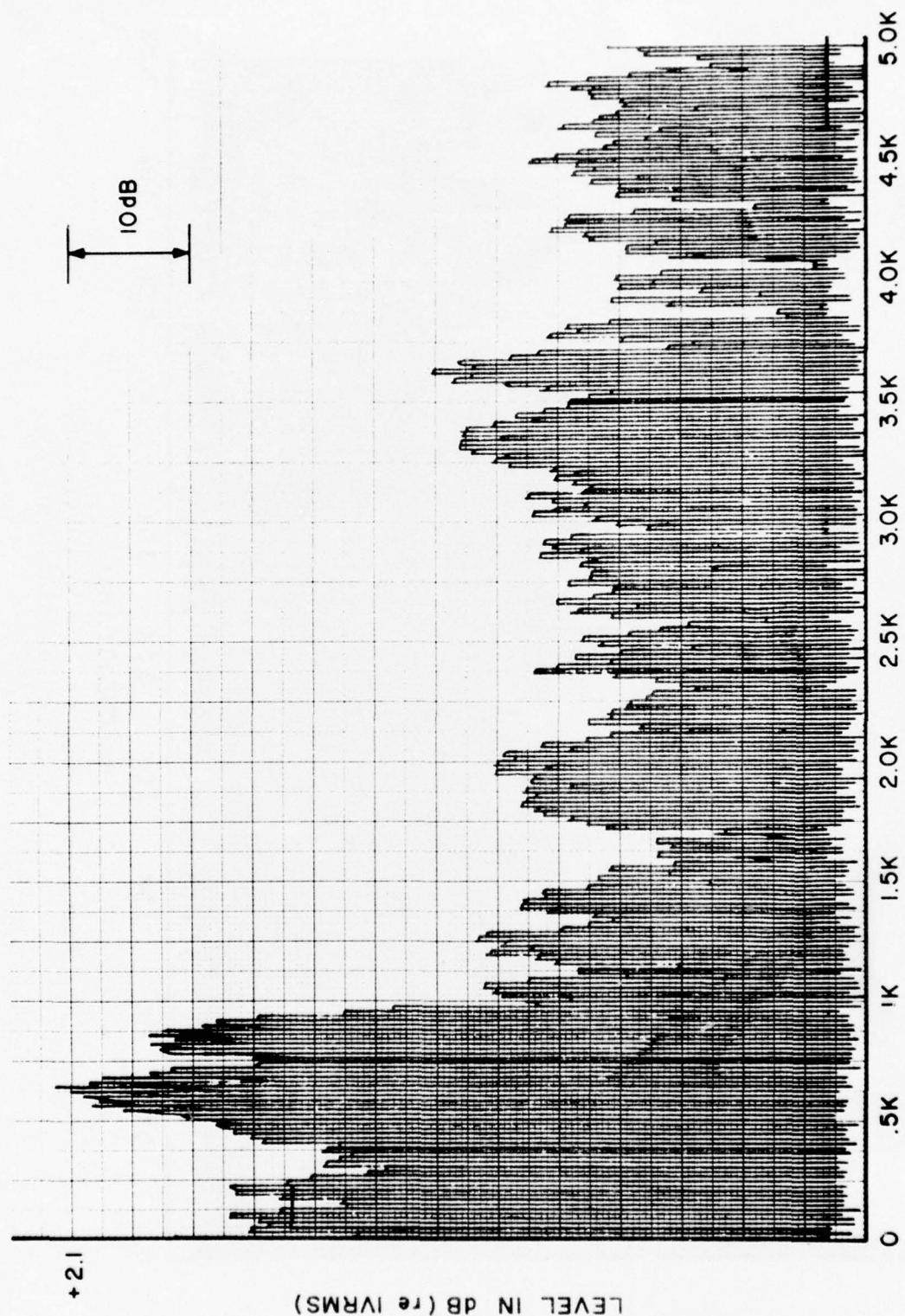


Figure 7. Spectral Energy Distribution Function for Vowel /ə/.

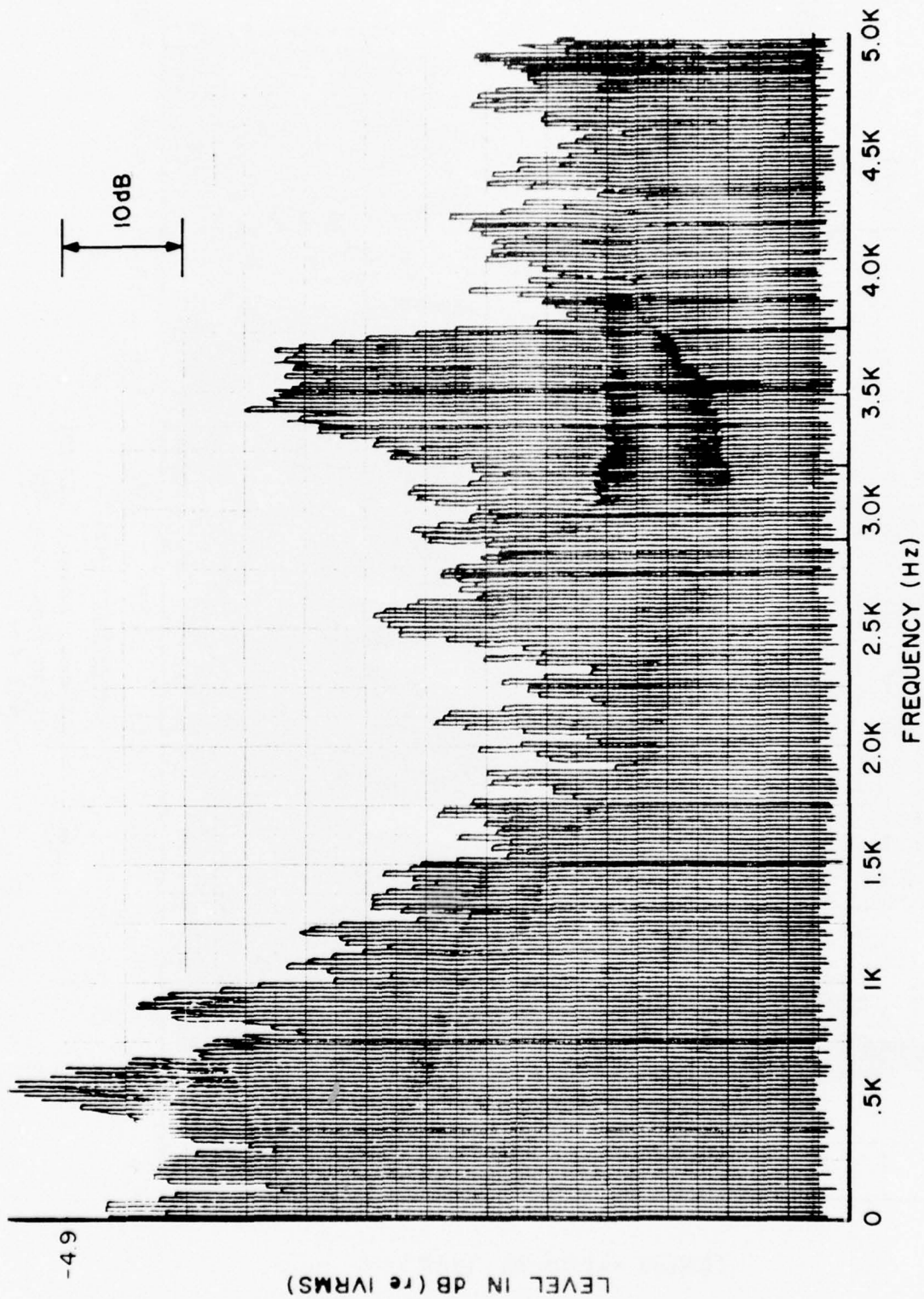


Figure 8. Spectral Energy Distribution Function for Vowel /o/.

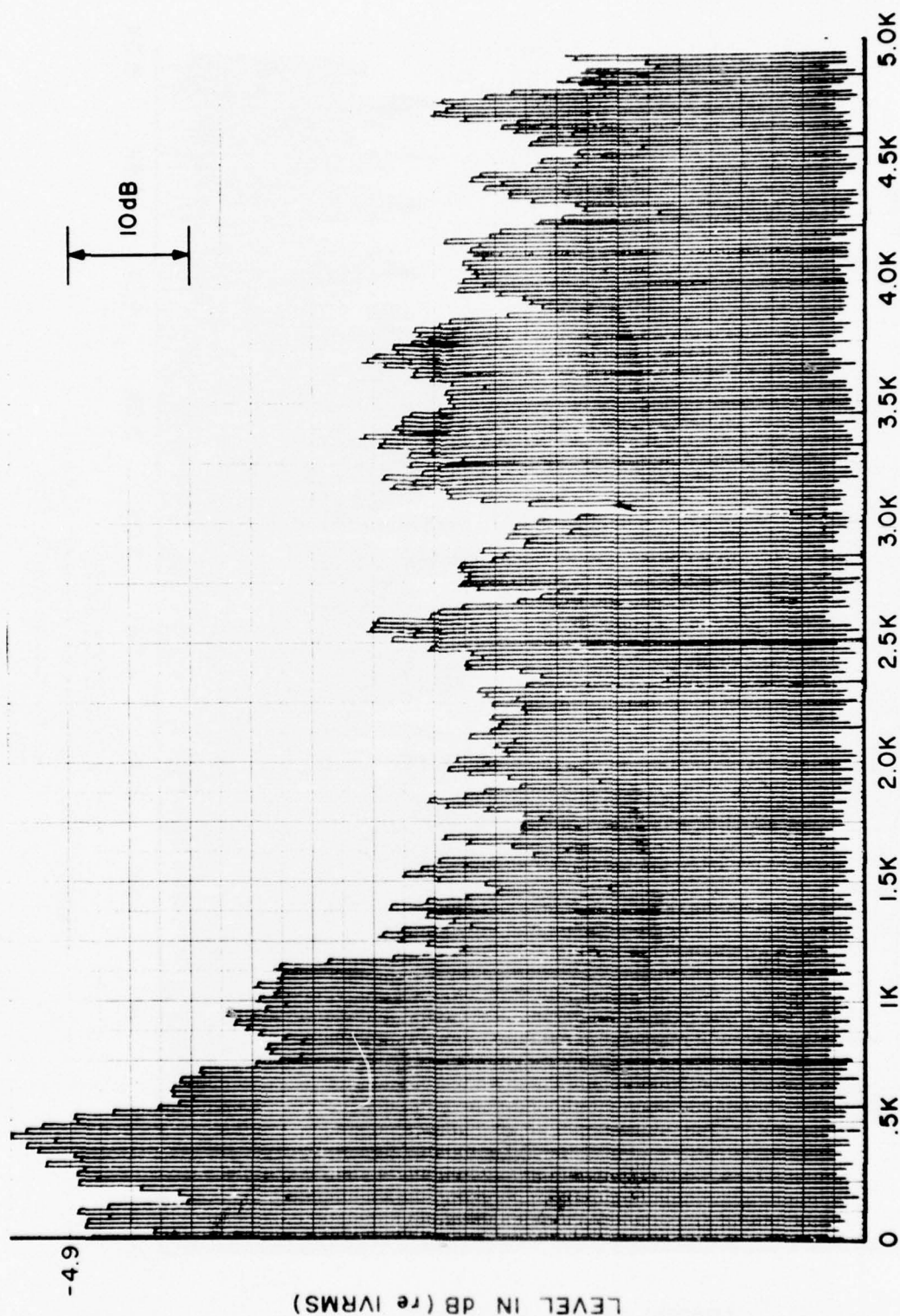


Figure 9. Spectral Energy Distribution Function for Vowel /u/.

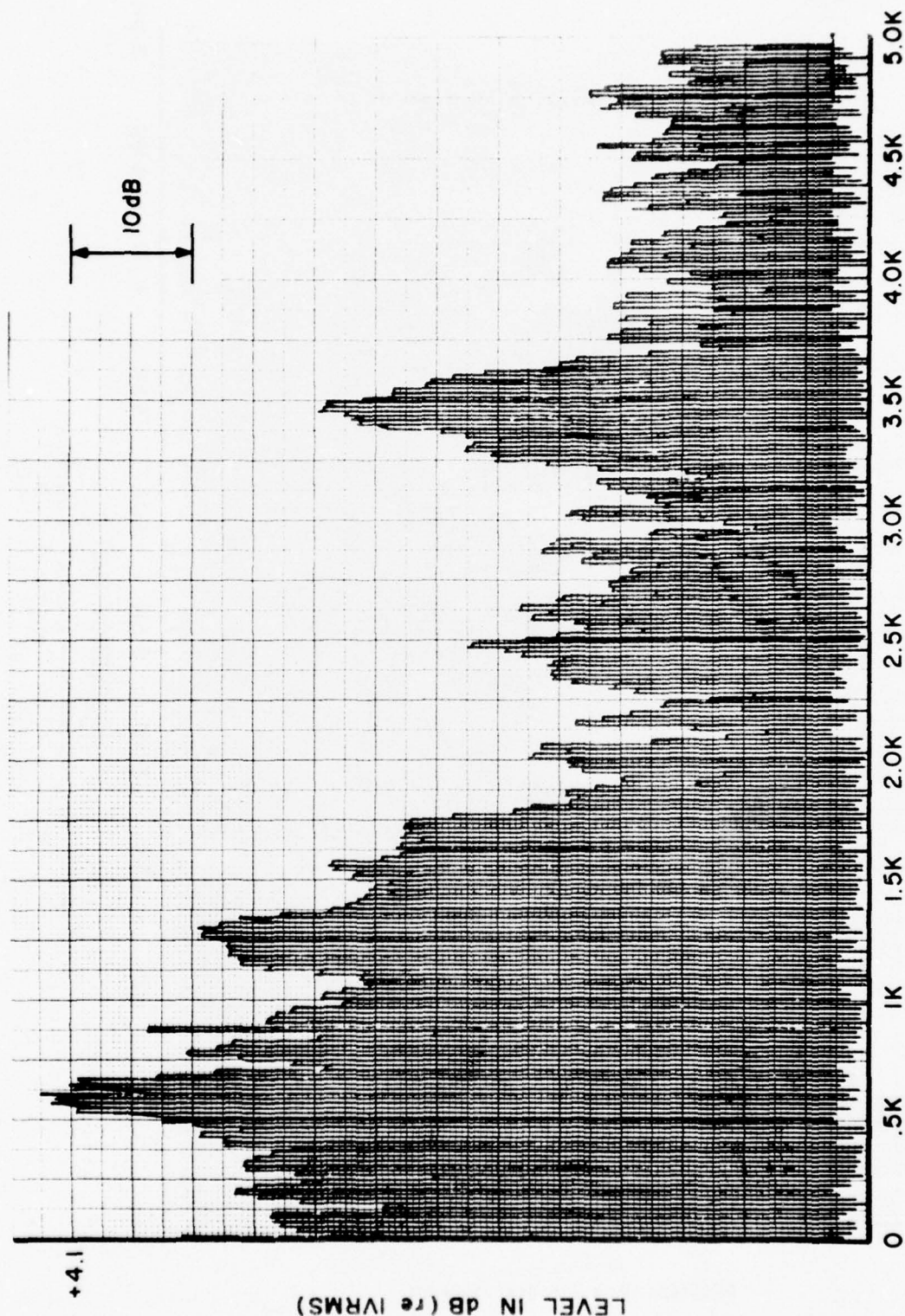


Figure 10. Spectral Energy Distribution Function for Vowel /r.

neuron stimulated at some frequency other than its CF might exhibit a response pattern characteristic of a "class" other than that to which it was assigned on the basis of its response when stimulated at its CF (Caspary, 1972; Mast, 1970; Moore and Cashin, 1974), the present report concerns itself only with those CN neurons that are classified as "primary-like" on the basis of their response at their CF.

A. Results

Figure 11 shows a comparison of the response patterns of a primary neuron (CF 673 Hz) and a "primary-like" cochlear nucleus neuron (CF 636 Hz) to three speech sounds. The level at which these sounds were presented was comparable for the two neurons, 80 dB SPL for the primary neuron and 85 dB SPL for the "primary-like" CN neuron. The threshold of the primary neuron at its CF was 54 dB SPL, that of the CN neuron was 50 dB SPL. As can be seen in Fig. 11, the agreement between the two neurons' response patterns ranges from excellent to poor. For the vowel /ε/ the two response patterns are virtually identical. The response of the CN unit, which was presented with a 5 dB SPL more intense signal, is relatively larger in amplitude than that of the primary unit. The timing of the firings within the response patterns are identical. For the vowel /a/, the response of the CN unit while simpler than the response of the primary unit still has represented within each pitch period the dominant interval found throughout each pitch period of the primary unit's response. Finally, the responses to the vowel /i/ differ in that the CN unit shows a complete suppression of response to /i/, while the primary unit shows a simple but well defined response pattern. As noted above, the signal presented to the CN unit was 5 dB SPL more intense than that presented to the primary unit. This complete suppression of neural activity when stimulated by certain vowel sounds (particularly those with significant energy content at the higher frequencies) is not uncommon in cochlear nucleus neurons, while it has not been found at all in eighth nerve units.

/ε/

/a/

/i/

CN 5/3/72 - 4 - 13

CN 5/3/72 - 4 - 13

CN 5/3/72 - 4 - 12

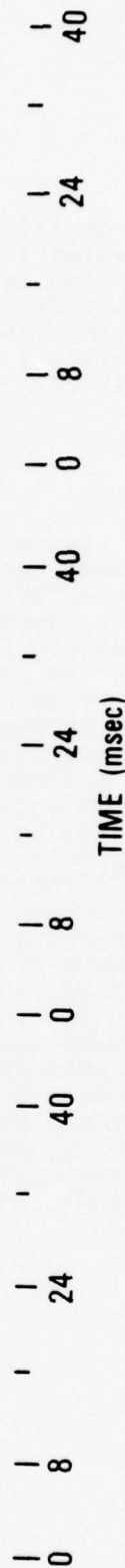
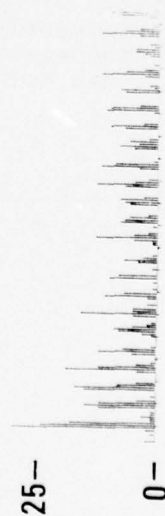


SPIKE COUNT

8thN 8/27/71 - 3 - 5

8thN 8/27/71 - 3 - 5

8thN 8/27/71 - 3 - 4



TIME (msec)

Figure 11. Comparison of Response Patterns of an Eighth Nerve Neuron (8/27/71-3; CF673 Hz) and a "Primary-like" Cochlear Nucleus Neuron (5/3/72-4; CF 636 Hz) to the Vowels /ε/; /a/; and /i/.

B. Discussion

Studies of the output from an analog cochlear model in response to vowel inputs indicated that one of the most important cues for the identification of the individual vowels was the temporal interval defined by the major peaks in the displacement pattern of the basilar membrane to the individual pitch periods of each vowel (Godfrey, 1972 a, b, 1974; Mundie and Moore, 1967, 1968 a, b, 1970). A psychoacoustic study provided evidence that sufficient information existed within a single pitch period to allow reliable identification of the vowel from which the pitch period was excerpted (Moore and Mundie, 1971). Measurements of the temporal value of these key intervals defined within a pitch period have shown them to be correlated with the formant values of the vowel being studied (Godfrey, 1974; Mundie and Moore, 1967).

Previous neurophysiological reports (Goldstein and Mundie, 1971, 1972; Mundie, et al., 1974) have shown that the firing pattern of the great majority, if not all, of eighth nerve units is modulated by the displacement pattern of that portion of the basilar membrane that the unit innervates. There was some indication in the data that a minority of the units studied may have had their response modulated by the velocity of the basilar membrane rather than the displacement. In those units whose response was modulated by the displacement of the basilar membrane, the key intervals present in the basilar membrane pattern were preserved in the neural firing pattern. Figure 11 shows that if the CN "primarylike" unit responded to the speech sound, it also preserved these key intervals in its response pattern.

RESPONSE ARRAY OF "PRIMARYLIKE" CN NEURONS TO VOWEL SOUNDS

In order to gain some insight into the pattern of activity generated within a population of "primarylike" CN neurons by specific vowel sounds, an array of seven neurons was composed for each vowel sound employed as a stimulus. The same seven neurons were used in generating the array for each of the ten vowel sounds. Figure 12 shows the response areas of the seven neurons. These neurons were selected so as to encompass within their composite response areas a frequency range that would include those frequencies at which the vowel stimuli had major concentrations of energy (see Figs. 1-10). The intensity at which the vowels were presented ranged between 60 and 85 dB SPL. The values for each neuron in the array are shown in Table I. In each array the neurons are ordered from lowest to highest CF.

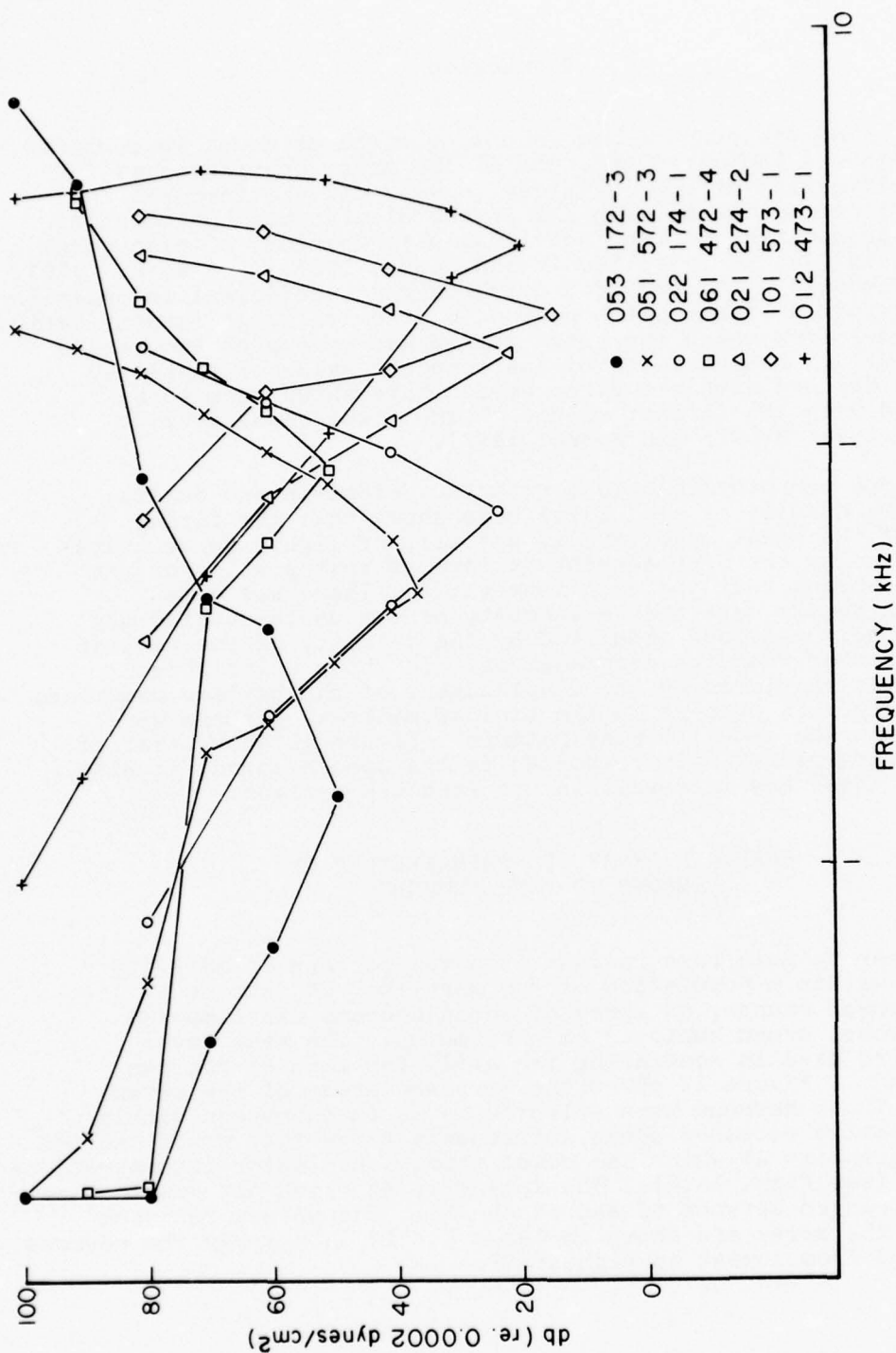


Figure 12. Response Areas of Seven CN "Primary-like" Neurons Used to Compose Response Arrays To Specific Vowel Sounds.

TABLE I

Neuron Ident. Number	CF (Hz)	Level in dB SPL At Which Vowels Were Presented
053-172-3	146	85
051-572-3	456	60
022-174-1	707	63
061-472-4	907	80
021-274-2	1696	60
101-573-1	2091	64
012-473-1	3032	60

A. Results

Figures 13-22 show the neural arrays for each of the vowel sounds used as stimuli. An overview of these arrays indicate some striking differences between the overall response patterns for the various vowels. In general terms, the distribution of activity across the array differs from vowel to vowel and allows a visual separation of the vowels. This variation in activity is a reflection of the response of the basilar membrane displacement and is correlated with the energy-frequency content of the vowels. Where there are clear intervals defined within each pitch period of the neural response, these intervals almost always correspond to either the pitch rate of the vowel or the pitch rate and a frequency equivalent to the first formant of the vowel. Because of the resolution at which the data was gathered and the limits within which the intervals can be measured by hand, there are no clear indications of intervals corresponding to second and third formants. There are, however, examples of very short interval (high frequency) activity being modulated at the vowel's pitch rate, e.g., the 2091 Hz neuron in the array for /i/ (Fig. 13) and the 1696 Hz neuron in the array for /æ/ (Fig. 16).

What follows is a more detailed description of the overall neural response for four of the vowels.

1. /i/ (Fig. 13) - The overall pattern shows two quite distinct areas of responsiveness separated by an area of essentially complete suppression. The response of the 146 Hz neuron is a very sharp, strong response that defines an interval of approximately 4.0 msec (250 Hz). The response of the 456 Hz neuron also defines this interval, although less strongly. The predominant interval in this response is about 7.8 msec, equivalent to the pitch rate of the vowel. This activity is followed by essentially complete suppression of activity in the 707 Hz and 907 Hz neurons. The 1696 Hz neuron shows a slight amount of neural activity occurring at the pitch rate of the vowel. The 2091 Hz neuron shows an increased amount of high frequency activity distributed in a relatively broad pattern occurring at the vowel's pitch rate. Finally the 3032 Hz neuron clearly defines the vowel's pitch rate with a sharp, localized burst of activity and has a less well defined burst of activity occurring about 4 msec later within each pitch period.

Examination of the spectral energy distribution for /i/ (Fig. 1) in conjunction with the response area plots for the neurons (Fig. 12) shows a correlation between the frequency-energy content of the signal and the neural response, i.e., the response areas of the 707, 907 and 1696 Hz neurons, which had little or no response, encompass a frequency region in which there is relatively little energy for /i/, consequently the magnitude of displacement of the basilar membrane for that region

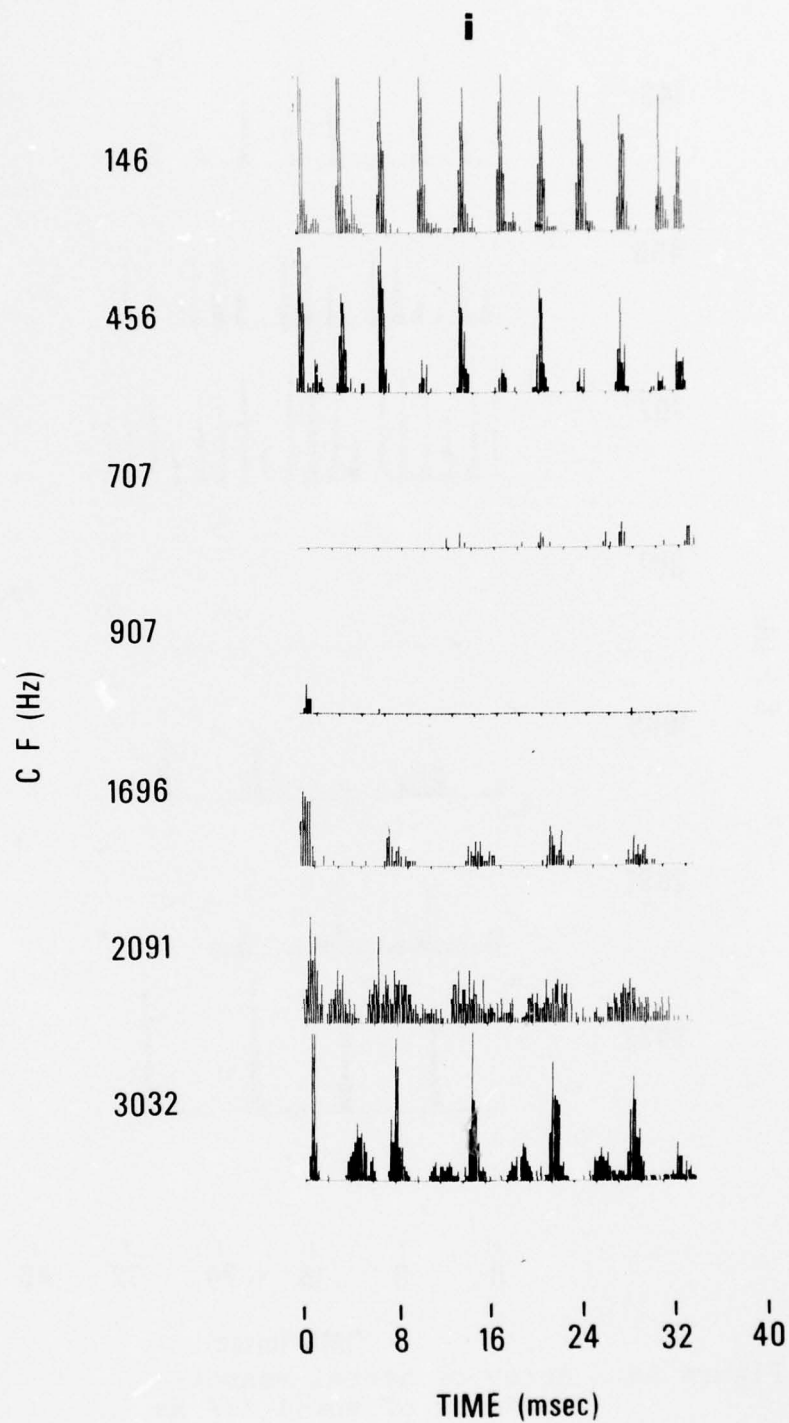


Figure 13. Array of neural response patterns to vowel /i/ as in the word "beet".

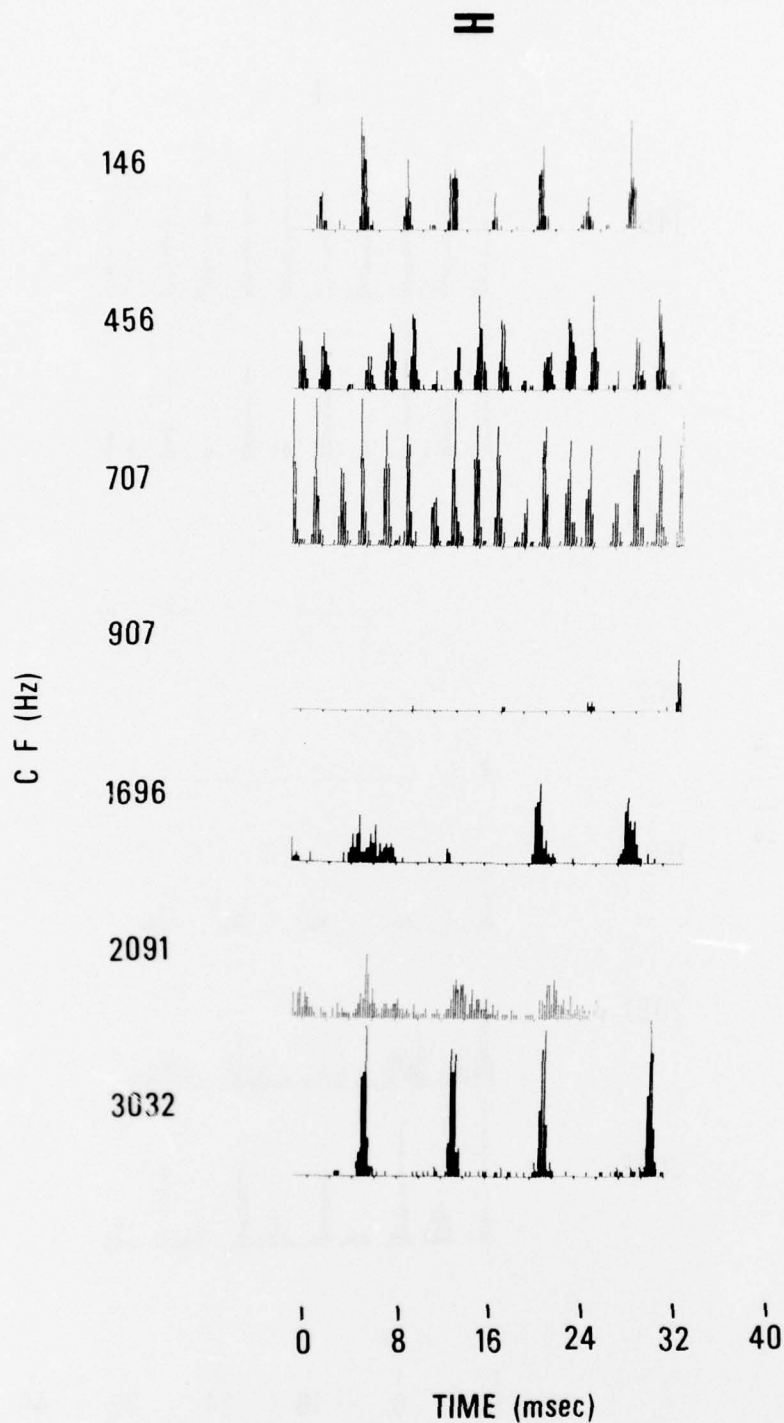


Figure 14. Array of neural response patterns of vowel /I/ as in the word "bit". This vowel was in the final position for the 1696 Hz neuron. The response to /I/ starts at about 15 msec.

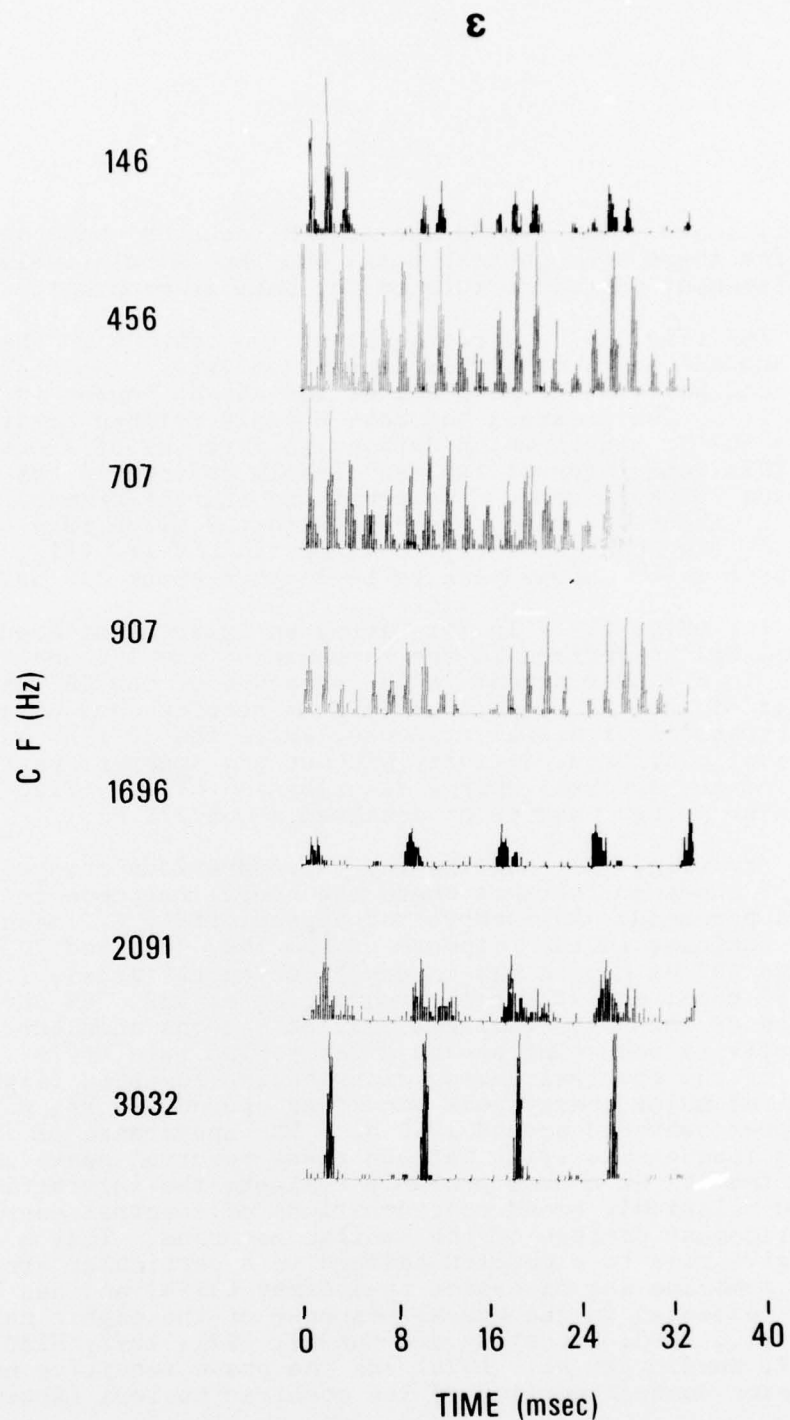


Figure 15. Array of neural response patterns to vowel /ε/ as in the word "bet". This vowel was in the final position for the 907 Hz neuron. The response to /ε/ starts at about 16 msec.

is relatively small. The 146 Hz and 3032 Hz neurons encompass areas in which there are spectral peaks and thus a relatively strong displacement pattern exists on the basilar membrane.

2. /æ/ (Fig. 16) - Here the first two neurons in the array (146 and 456 Hz) show little neural activity. Note that only the second half of the response of the 456 Hz neuron is the response to /æ/. The greatest and most sharply defined activity is shown by the 907 Hz neuron which defines an interval of about 1.3 msec (770 Hz). This same interval is less clearly defined in the response pattern of the 707 Hz neuron. The remaining neurons primarily define an interval of about 8.2 msec, equivalent to the pitch rate of /æ/. Examination of the spectral energy distribution of /æ/ (Fig. 4) shows the first major energy peak to be located about 725 Hz.

3. /u/ (Fig. 21) - In this array an interval of about 2.6 msec (390 Hz) is defined in the response of the 146 and 456 Hz neurons, and to a lesser extent in the response of the 707 Hz neuron. The responses of the 907, 1696, and 2091 Hz neurons show an almost complete suppression of neural response, while the 3032 Hz neuron shows low level continuous activity without any apparent patterning. Examination of the spectral energy distribution of /u/ (Fig. 9) shows its major energy peak to be centered about 375 Hz.

4. /r/ (Fig. 22) - Unlike the three previous arrays, the array for /r/ shows no instance where the neural response is completely suppressed. An interval of approximately 1.7 msec (588 Hz) is dominant in the response of the 146, 456, and 707 Hz neurons. The 907 Hz neuron has intervals of approximately 1.53, 1.3, and 1.07 msec, equivalent to frequencies of 653, 769 and 935 Hz. The responses of the 1696, 2091 and 3032 Hz neurons show bursts of neural activity occurring at the pitch period rate of /r/. Examination of the spectral energy distribution function (Fig. 10) shows the first major energy peak occurring around 600 Hz, with the second peak centered around 1250 Hz. The appearance of intervals representing frequencies lying between these spectral peaks in the response of the 907 Hz neuron probably reflects the interaction of these two relatively broad concentrations of spectral energy in the displacement pattern of the basilar membrane. That a complex signal may give rise to a complex pattern on a particular area of the basilar membrane was discussed by Godfrey (1974) and has been shown to be reflected in the neural response of the eighth nerve (Brugge, et al., 1969; Goldstein and Mundie, 1971, 1972; Hind, et al., 1967; Mundie, et al., 1974) and the phase sensitive neurons of the anterior ventral portion of the cochlear nucleus (Rose, et al., 1974).

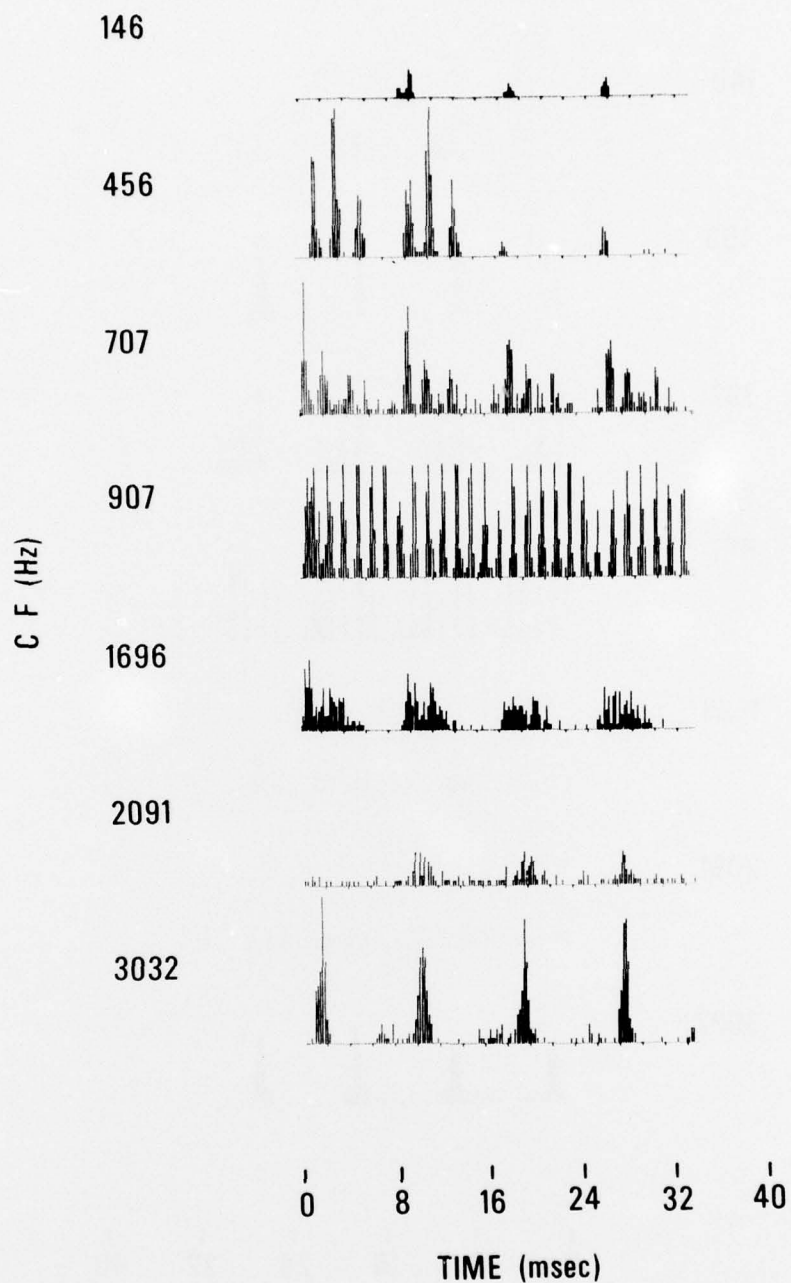


Figure 16. Array of neural response patterns to vowel /æ/ as in the word "bat". This vowel was in the final position for the 456 Hz neuron. The response to /æ/ starts at about 18 msec.

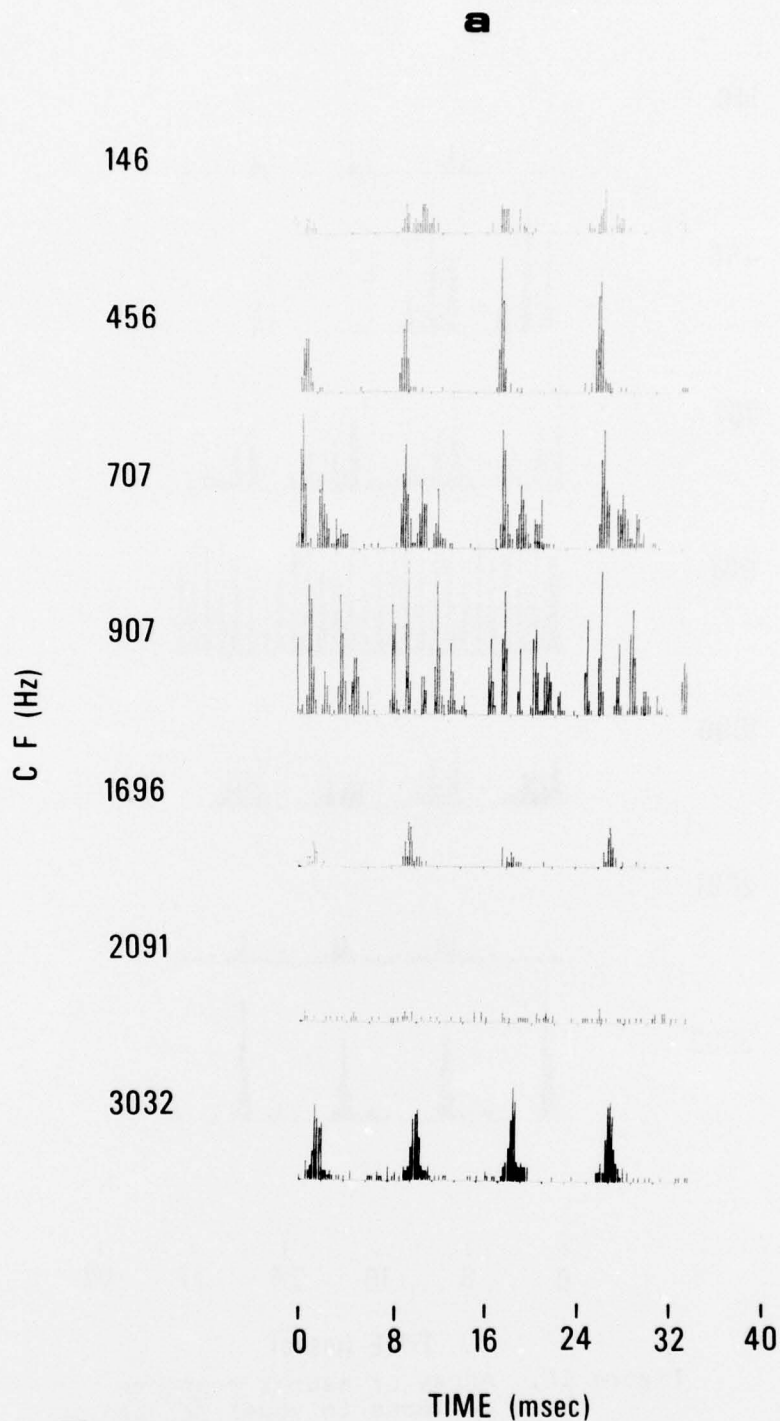


Figure 17. Array of neural response patterns to vowel /a/ as in the word "hot".

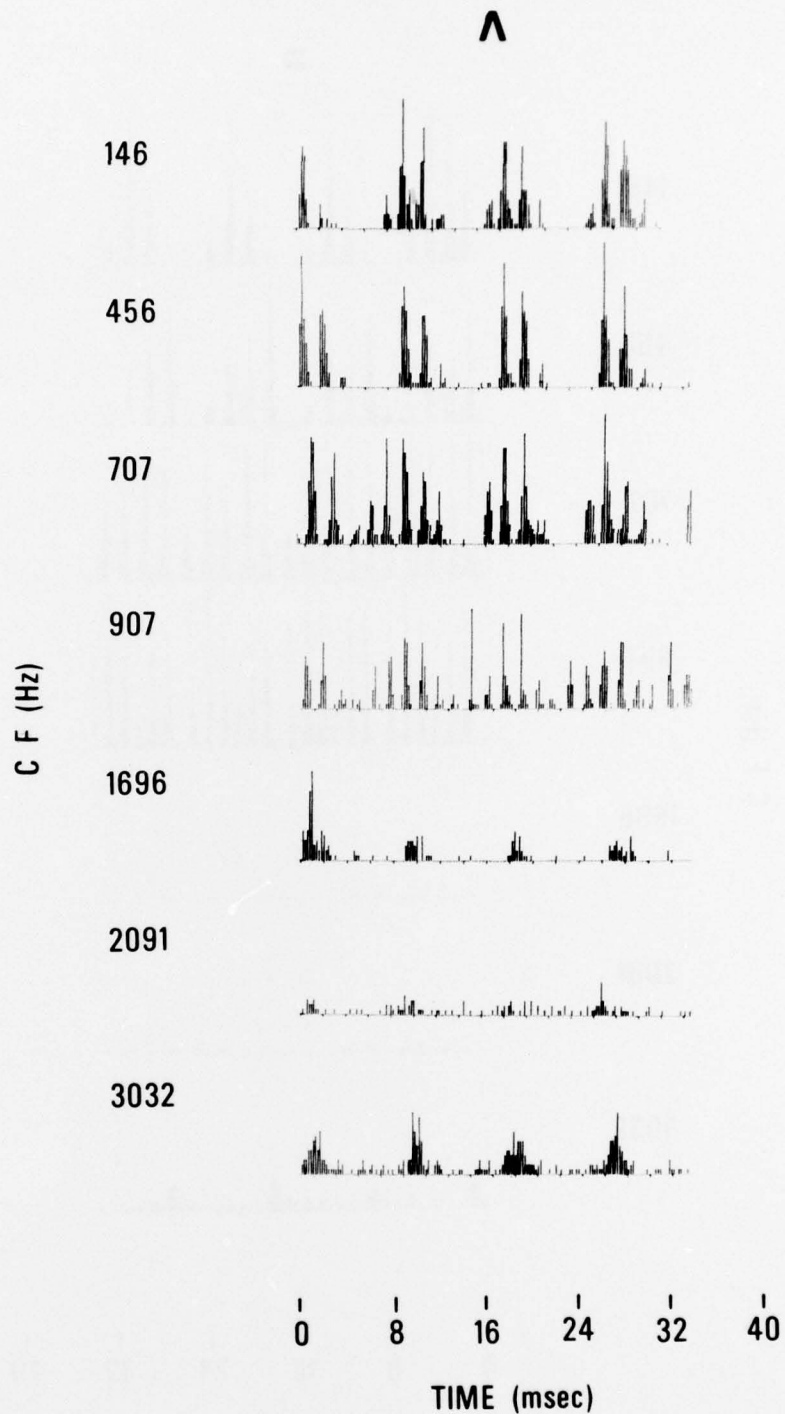


Figure 18. Array of neural response patterns to vowel /Λ/ as in the word "but". This vowel was in the final position for the 707 Hz neuron. The response to /Λ/ starts at about 16 msec.

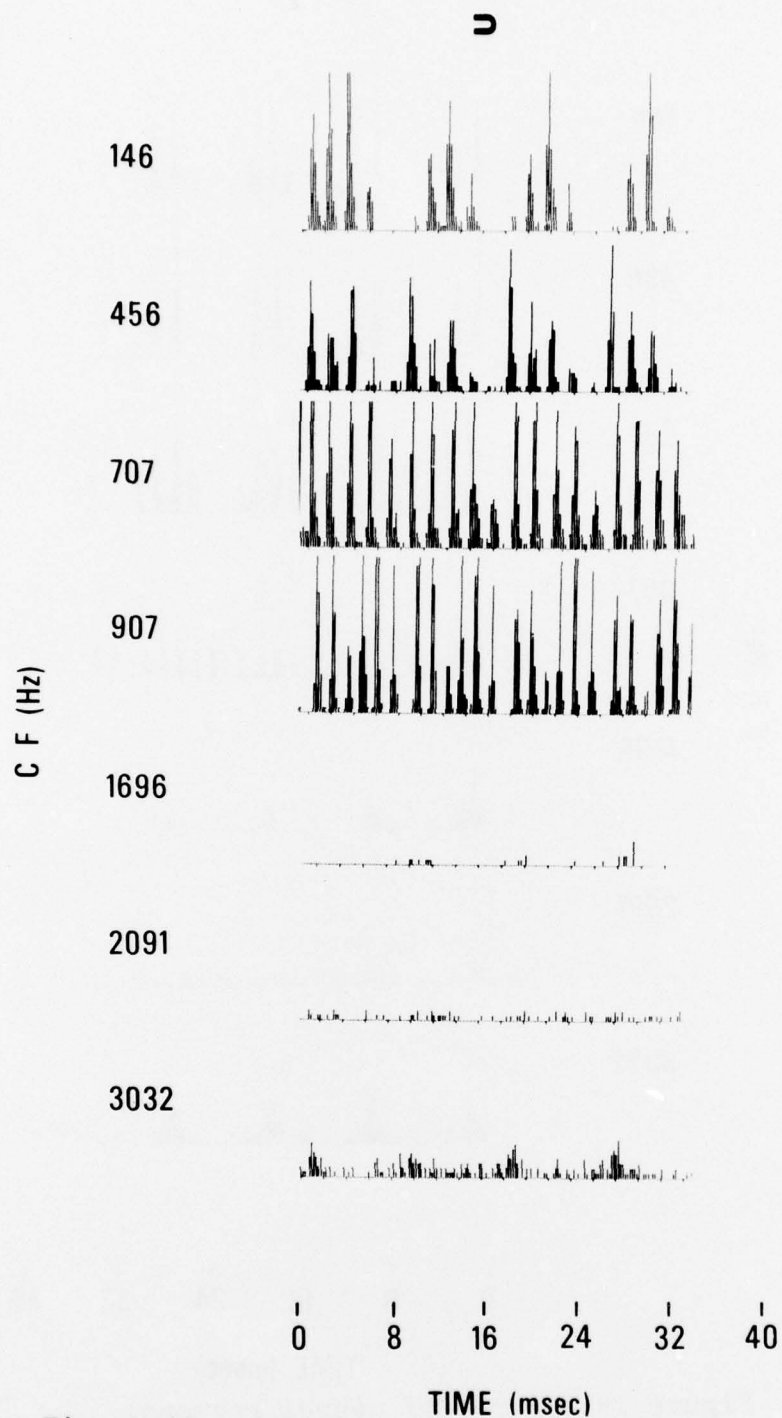


Figure 19. Array of neural response patterns to vowel /ɔ/ as in the word "caught".

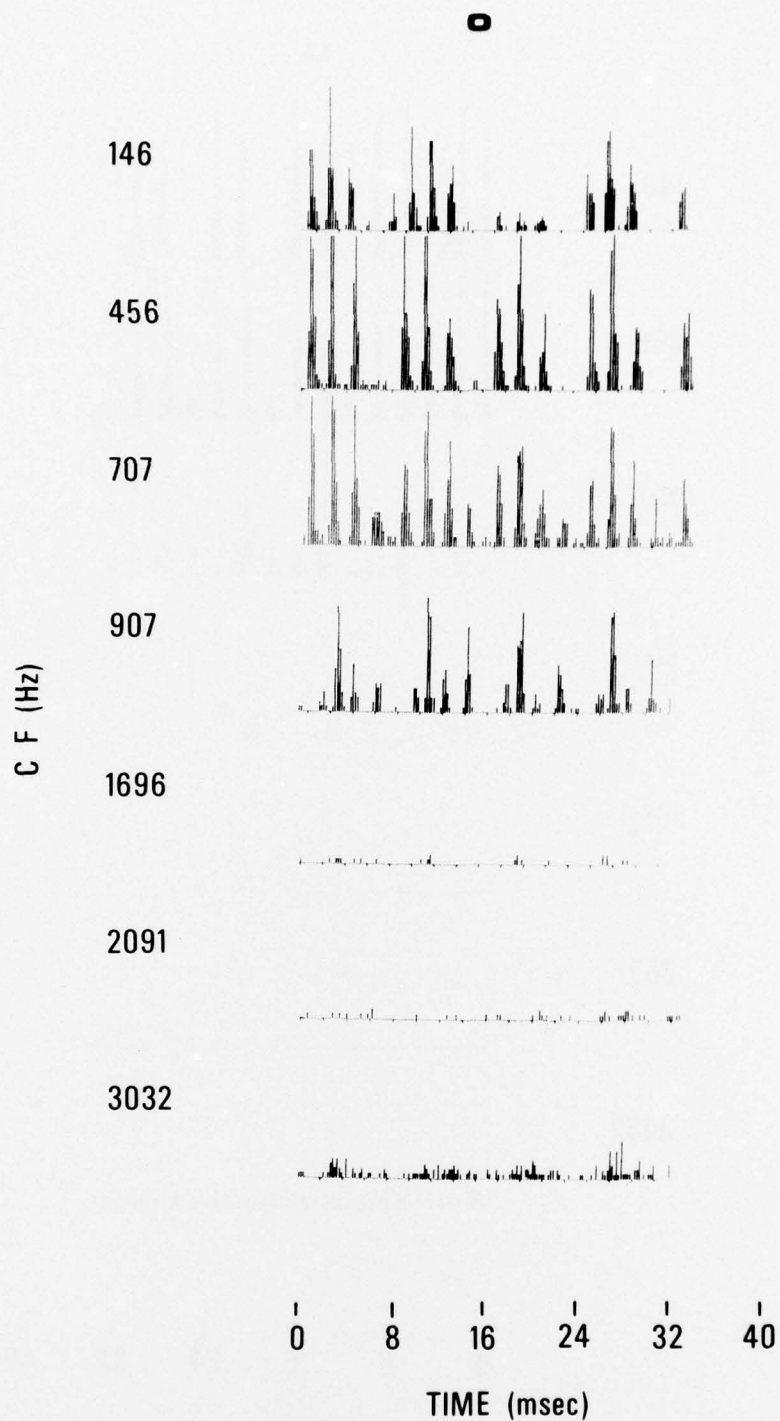


Figure 20. Array of neural response patterns to vowel /o/ as in the word "boat". This vowel was in the final position for the 146 Hz neuron. The response to /o/ starts at about 18 msec.

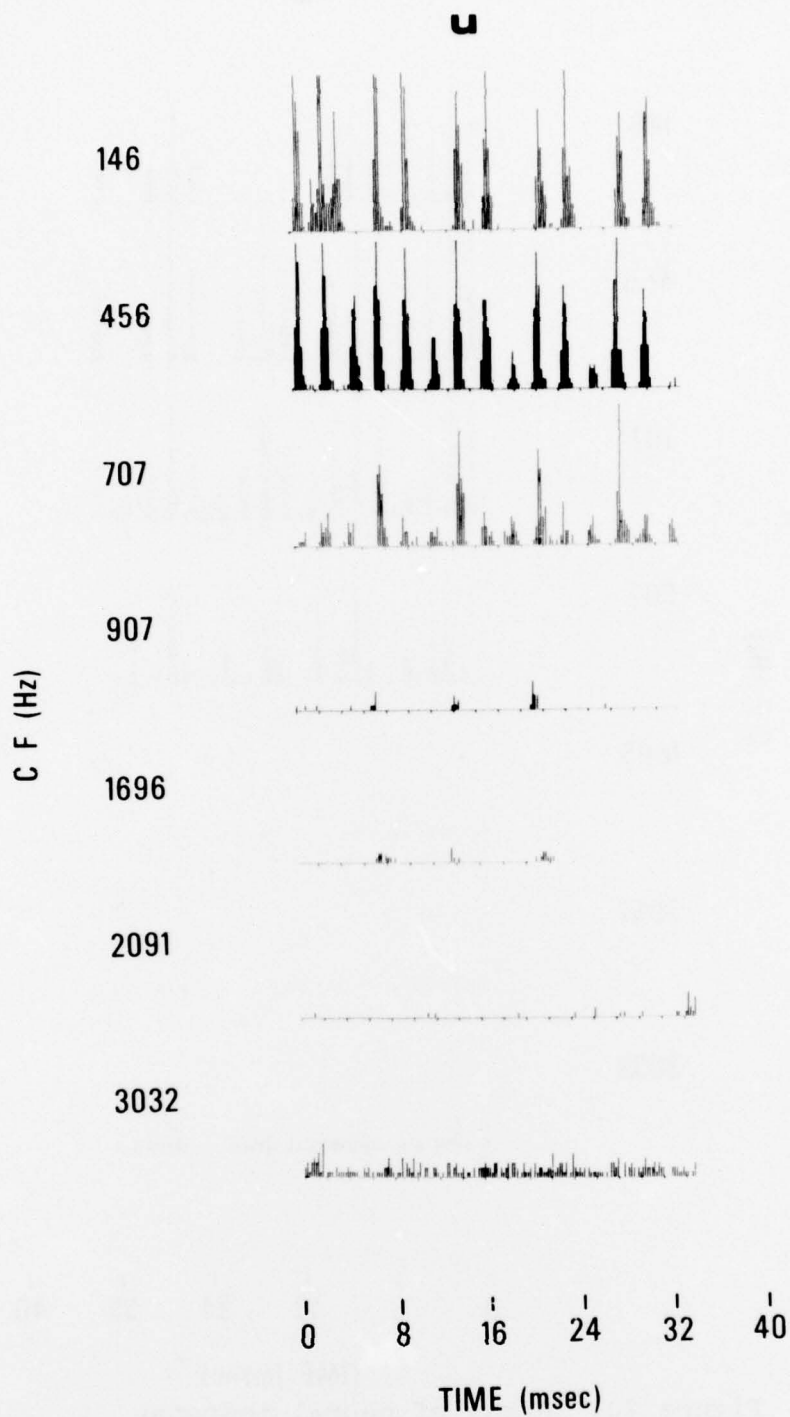


Figure 21. Array of neural response patterns to vowel /u/ as in the word "boo".

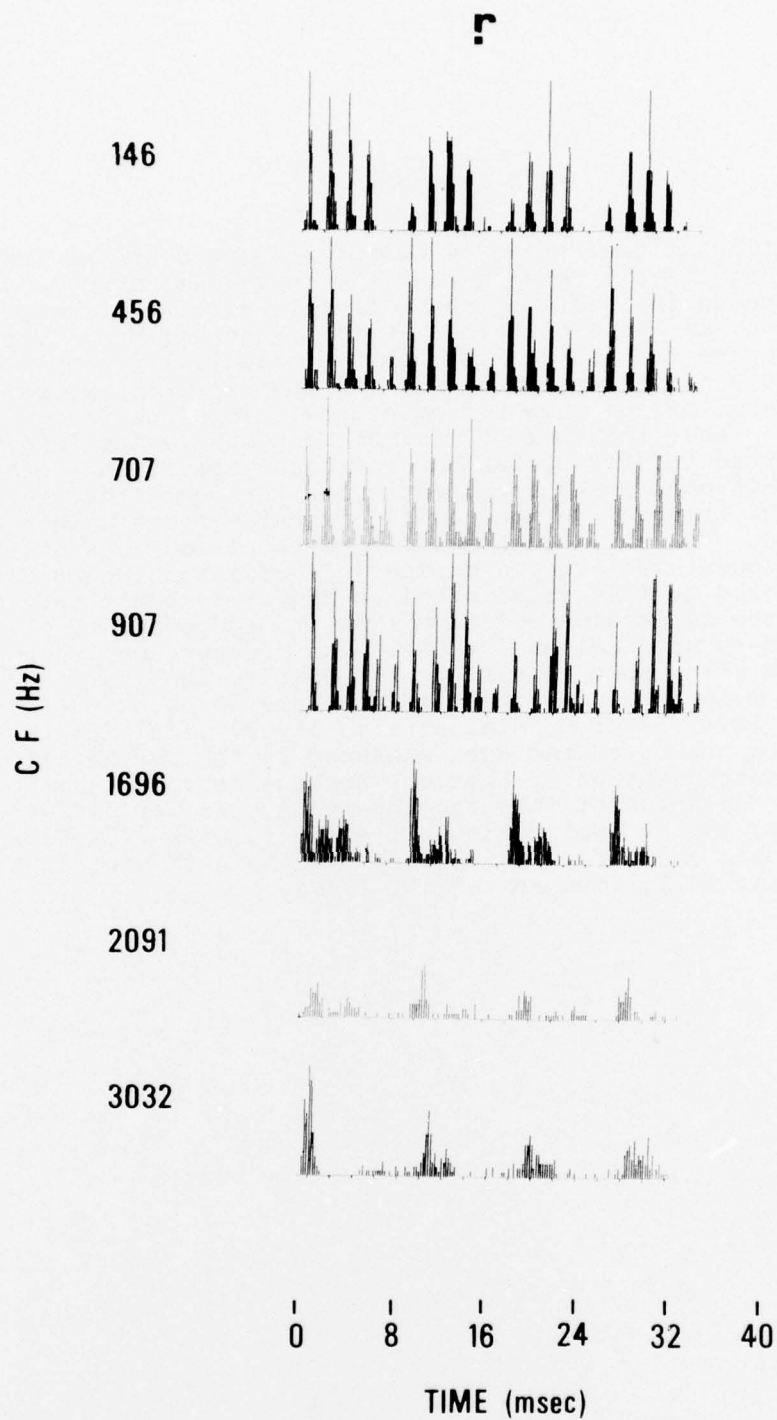


Figure 22. Array of neural response patterns to vowel /r/ as in the word "burr".

B. Discussion

Examination of the arrays of neural responses to the ten vowel sounds used as stimuli reveals that the individual arrays can be distinguished on the basis of their overall pattern of responsiveness, as well as on the basis of details within each pattern. The existence of regions where the neural response was essentially completely suppressed by a particular vowel was the most striking gross cue in separating some of the vowels from others. This cue in combination with the fact that the area of maximum response varied from vowel to vowel served to distinguish one response array from another. The key cue within each array for identifying the vowel that gave rise to it was the interval defined by the neural firings within each pitch period. For all the arrays the pitch period rate of the appropriate vowel was clearly marked. In addition, where dominant intervals could be identified within a neural response they faithfully reproduced the intervals defined within the responses of primary auditory fibers with comparable CFs. The primary unit responses in turn have been shown to reflect the displacement pattern of the basilar membrane in response to the same vowel stimuli (Goldstein and Mundie, 1971, 1972; Mundie, et al., 1974). The fact that these intervals are preserved and even enhanced in the firing patterns of at least a subpopulation of cochlear nucleus neurons lends credence to the argument that the important cues for differentiating vowel sounds, and by implication all auditory signals, lie in the temporal domain and not in the frequency domain (Moore, 1974; Mundie and Goldstein, 1971; Nordmark, 1968, 1970).

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